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Nest tree characteristics of Grey-headed Woodpeckers (*Picus canus*) in boreal forests

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Woodpeckers are important species in forest ecosystems because they make tree cavities that are microhabitats for several other taxa. However, even in boreal areas where most tree cavities are made by woodpeckers, the properties of woodpeckers' nest trees and cavities are poorly known. We studied nest tree characteristics of the Grey-headed Woodpecker (*Picus canus*) in a 170-km^2 forest-dominated area in southern Finland during 1987–2019. The data included 76 nest trees with 80 nest cavities in five different tree species. During the study period, 44% of all nesting attempts were in old cavities. Nests were found in four forest types, but the proportions of nest tree species differed between them. In all, aspen (*Populus tremula*) with 70% of nest trees, and with 71% of nest cavities was the dominant cavity tree species. Most nest trees (85%) were dead or decaying, and most cavities (70%) were excavated at visible trunk injury spots. The mean diameter of a nest tree at breast height (DBH) was 37.2 cm and the mean height of a cavity hole was 7.8 m; these were significantly positively correlated. The results highlight the importance of large aspens as nest cavity sites for the species. Conservation and retention of groups of large aspens in main habitats, including clear-cuts, are important for continuous availability of nest trees. This applies particularly to managed boreal forest landscapes where scarcity of suitable trees may be a limiting factor for the species.

1. Introduction

Woodpeckers are proposed as indicator or keystone species of forest structural complexity and species diversity (Mikusiński *et al.* 2001, Roberge *et al.* 2008, Pakkala *et al.* 2014). The properties of nest trees are important for woodpeckers themselves, especially to ensure the excavation of strong and safe cavities, but also for several other cavity-nesting animals like mammals, birds and invertebrates that use these cavities afterwards (Jones *et al.* 1994, Drever *et al.* 2008, Cockle *et al.* 2011, Siitonen & Jonsson 2012, Hardenbol *et al.* 2019). Most tree cavities in the boreal zone are suggested to be made by woodpeckers (Aitken & Martin 2007, Cockle *et al*. 2011, Andersson *et al.* 2018), and thus are very important microhabitats in these forests.

In this study, we investigated nest tree characteristics of the Grey-headed Woodpecker (*Picus canus*) in a boreal forest landscape dominated by managed coniferous forests. The species has a wide Eurasian distribution, and it prefers deciduous tree dominated or mixed forests with edges and openings (Dementiev & Gladkov 1966, Glutz von Blotzheim & Bauer 1980, Cramp 1985, Blume 1996, Saari & Südbeck 1997). Moreover, the Grey-headed Woodpeckers mostly use injured or decaying deciduous trees for excavating their nest cavities (Conrads & Herrmann 1963, Glutz von Blotzheim & Bauer 1980, Cramp 1985, Südbeck 2009), but published information of the nest tree characteristics is scarce for boreal forests.

We explored and documented the main characteristics of the nest trees and forest types using a large data set from southern Finland. As the species number and composition of potential nest cavity trees greatly differ between boreal and more southern forest areas (Hågvar *et al.* 1980, Remm & Lõhmus 2011, Wesołowski & Martin 2018, Pakkala *et al.* 2019), we anticipate that detailed knowledge of the characteristics of nest trees and of their spatial variation in different types of forests and in different geographical locations is important for explicit guidelines for forest management and conservation.

2. Material and methods

2.1. Study area

The study area (170 km^2) is located within the southern boreal vegetation zone in southern Finland (around 61°15’ N; 25°03’ E; see Pakkala *et al.* 2017). It is dominated by managed coniferous forests on mineral soils, with a mixture of stands of different ages, and many small oligotrophic lakes. Human settlements in the area are scarce. The forest management in the study area aims for timber production, and the prevailing harvesting method is clear-cutting.

2.2. Grey-headed Woodpecker nest tree surveys

As part of an intensive population study of forest bird species, especially woodpeckers, Grey-headed Woodpecker nests and nest trees were searched within the study area each year during the period 1987–2019. The annual census typically lasted from early April to mid-July and included the mapping of woodpecker territories within the study area with simultaneous efforts to locate potential nesting sites by observing the behaviour of the woodpeckers, and by searching for nests during the breeding season (described in detail in Pakkala 2012 and in Pakkala *et al.* 2014, 2017).

Annual territory locations and their approximate borders were defined by information from observed locations and movements of the woodpeckers, and by the presence of the nest sites. The centres of territory sites for the study period were defined by locations of annual territories. The estimated total number of territory sites during the study period was 29 with a mean of about 15 annually occupied territories within the whole study area.

Based on the annual occupancy rates of territories and estimates of nesting success (T. Pakkala, unpublished data), the data in this study covered ca. 20% of all nesting attempts within the study area during the study period. All surveys of the nest trees and cavities (see below) were carried out by author TP.

2.3. Nest tree and cavity data

All the trees with cavities where nesting of the Grey-headed Woodpecker was observed during the study period were classified as nest trees. We included only those cavities where Grey-headed Woodpeckers reached at least the egg-laying phase, e.g. we omitted cavities where nesting attempts were interrupted during excavation, although they would have contained a seemingly complete nest cavity. The observed nest trees and cavities were annually followed during the study period to check their reuse by the Grey-headed Woodpecker.

The species of all the detected nest trees was identified. At each nest tree location, the main forest type of the site was defined in the field, based on the classifications of Finnish forest and peatland types (Cajander 1949, Laine *et al*. 2012). Additionally, the proportions of forest types within a 700-m radius from the centre of each territory site, corresponding the approximate mean territory size during the breeding season (T. Pakkala, unpublished data), were calculated using land cover and forest classification data (Vuorela 1997), digital topographic maps of the area made by the National Land Survey of Finland, aerial photographs and field information from the study area (see Pakkala *et al.* 2014).

We used three classes of the condition of the nest tree (see also Pakkala *et al.* 2018). 1) Healthy: mainly a vital tree with no signs of decay; small wounds or damages by external factors possible. 2) Decaying: tree alive, but clear signs of decay visible, e.g. dead branches in the crown and/or top defoliation or needle loss detected. 3) Dead: tree not alive. At the tree level, we used the condition from the year when the first cavity with a nesting attempt was observed during the study period. At the cavity level, the first nesting attempt year of each cavity was applied to describe the condition of the nest tree.

The cavity type was divided to two classes whether the cavity was in the main trunk, or in branch of the tree. We also assessed visually whether the cavity opening was excavated to an injury spot or a healthy site in the bark layer of the tree. Injury spots included, besides various wounds or scars in the trunk of tree, also basal areas at the sites of broken or fallen branches.

Nest tree diameter at breast height (DBH, 1.3 m above the ground) in the first year of nesting was used in the analysis. The heights of cavity holes < 4.0 m were measured either with a rigid measuring tape, a telescopic pole or a long stick of known length with an accuracy of 0.1 m. Heights between 4.0 m and 6.0 m were estimated by measuring the 4.0 m level and then estimating the remaining height, with an accuracy of 0.2–0.5 m. Heights > 6.0 m were estimated by a standard stick method (West 2009) with an accuracy of 0.5 m; 2–3 repeated measurements of the same cavity from different directions were done to decrease the error in measurements.

2.4. Statistical methods

Forest type and condition of the nest tree between the respective groups were compared with goodness-of-fit tests. The distribution of DBH and the height distribution of the cavity holes in various tree species deviated from normal distribution because of skewness and/or kurtosis, and therefore, median-based Kruskal-Wallis or Mann-Whitney tests were used in the comparisons of DBH and height of the cavity holes between groups. In post hoc comparisons between pairs after a significant result, either a Bonferroni-corrected level $p < 0.05$ in the comparisons of proportions (goodness-of-fit tests) or Dunn's test with Bonferroni correction (Kruskal-Wallis tests) was used. Spearman's rank correlation coefficient was used in testing the dependence between the DBH and height of the cavity holes. All statistical analyses were performed with IBM SPSS Statistics 25.

3. Results

3.1. Nest tree species and their forest types

A total of 76 nest trees of five deciduous tree species, 80 nest cavities, and 118 nesting attempts were found in the study (Table 1). Aspen (*Populus tremula*) was dominant (70–76%) in the tree, cavity, and nesting attempt numbers. Other tree species were birch (*Betula* spp.), Scots pine (*Pinus sylvestris*), grey alder (*Alnus incana*), and black alder (*Alnus glutinosa*), and they were clearly less abundant (Table 1). The Grey-headed Woodpeckers mainly used the trunk of the tree as the cavity excavation site, and only two cavities (2.5%) were in a large branch of the tree; both were in aspen.

Grey-headed Woodpeckers used more than one nest cavity in three of the nest trees (4% of all nest trees) during the study period. These multi-cavity trees were all aspens; in two trees two cavities, and in one tree three cavities were used in separate years. The observed 80 cavities included 66 new cavities, 10 cavities in which the first detected nesting attempt definitely was in an old cavity, and 4 cavities in which it probably was in an old cavity. Moreover, in later study years, 38 nesting attempts of Grey-headed Woodpeckers were recorded in

Table 1. Number of nest tree species of the Grey-headed Woodpecker and their percentages (in parentheses) in cavity trees, cavities, and nesting attempts (nestings).

Tree species	Trees	Cavities	Nestings
Aspen (*Populus tremula*)	53 (70)	57 (71)	90 (76)
Birch (*Betula* spp.)	11 (14)	11 (14)	14 (12)
Grey alder (*Alnus incana*)	4 (5)	4 (5)	5 (4)
Black alder (*Alnus glutinosa*)	2 (3)	2 (2)	2 (2)
Scots pine (*Pinus sylvestris*)	6 (8)	6 (8)	7 (6)
Total	76 (100)	80 (100)	118 (100)

Table 2. Number and percentage (in parentheses) of Grey-headed Woodpecker nest trees in different forest types. The first row of each tree species shows the percentage of forest type for each cavity tree species (summing up to 100% for tree species over forest types). The second row shows the percentage of each cavity tree species of all tree species within the respective forest type (summing up to 100% within the forest type). The percentage of forest types (last row) represent their percentages of the total area in the 29 territory sites. The four forest types: MT = moist spruce dominated forests on mineral soil; OMT = moist mixed or deciduous tree-dominated forests on mineral soil; VT = dry pine dominated forests on mineral soil; SWAMP = deciduous tree-dominated, or mixed swamp forests on peatland soil.

Nest tree species	MT	OMT	VT	SWAMP
Aspen (*Populus tremula*)	40 (75)	12 (23)	1 (2)	0 (0)
	(83)	(92)	(14)	(0)
Birch (*Betula* spp.)	6 (55)	1 (9)	2 (18)	2 (18)
	(13)	(8)	(29)	(25)
Grey alder (*Alnus incana*)	0 (0)	0 (0)	0 (0)	4 (100)
	(0)	(0)	(0)	(50)
Black alder (*Alnus glutinosa*)	0 (0)	0 (0)	0 (0)	2 (100)
	(0)	(0)	(0)	(25)
Scots pine (*Pinus sylvestris*)	2 (33)	0 (0)	4 (67)	0 (0)
	(4)	(0)	(57)	(0)
Total (n = 76)	48 (63)	13 (17)	7 (9)	8 (11)
	(100)	(100)	(100)	(100)
Percentage of forest type in territory sites	63	8	18	11

previously observed cavities. Thus, the percentage of cavity reuse was 41–44%.

The 76 nest trees were found in four main types of forests (Table 2). Forests on mineral soils included 1) moist spruce-dominated forests of *Myrtillus* type (MT); 2) the more fertile, moist mixed forests of *Oxalis-Myrtillus* type (OMT), in which we also included the less common class of moist and deciduous tree-dominated forests of the *Oxalis-Maianthemum* type; and 3) dry pine-dominated forest of *Vaccinium* type (VT). Forest peatlands included 4) both deciduous tree-dominated, and mixed swamps (SWAMP) that were combined to a single class.

The use of the MT was very similar both at the nest tree and the territory scale (63%). However, the percentages of the four forest types collectively differed from the expected percentages within the study area (goodness-of-fit test: χ^2 = 11.7, p = 0.009, df = 3). OMT was favoured in relation to its area, but the observed percentage of nest trees was lower than expected in VT (Table 2).

Nest tree species depended on forest type: aspen was a dominant in moist forests (83–92%), but in dry forests Scots pine (67%), and in peatland forests alders (75% of nest trees) were most common nest trees (Table 2). These differences in distributions of nest trees were significant (χ^2 = 88.0, p <

Table 3. Number and percentage (in parentheses) of nest tree species of the Grey-headed Woodpecker according to tree condition. The condition is the situation when the first nesting attempt during the study period was observed in the tree.

Nest tree species	Tree condition		
	Alive, healthy	Alive, decaying	Dead
Aspen (*Populus tremula*)	11 (21)	31 (58)	11 (21)
Birch (*Betula* spp.)	0 (0)	0 (0)	11 (100)
Grey alder (*Alnus incana*)	0 (0)	0 (0)	4 (100)
Black alder (*Alnus glutinosa*)	0 (0)	1 (50)	1 (50)
Scots pine (*Pinus sylvestris*)	0 (0)	2 (33)	4 (67)
Total	11 (14)	34 (45)	31 (41)

0.001, df = 12), mainly due to proportionally higher amounts of aspens in moist forests and both alder species in SWAMP compared with other forest types (Bonferroni-corrected $p < 0.05$ for these pairwise differences, Table 2).

3.2. Condition of the nest trees and cavity spots

The Grey-headed Woodpeckers selected mostly decaying (45%) or dead (41%) trees for their nests; only 15% of nest trees were healthy (Table 3). However, the condition distributions between aspen, the dominant nest tree species, and all the other tree species combined, significantly differed from each other ($\chi^2 = 29.4$, $p < 0.001$, $df = 2$); and the pairwise differences in all condition classes were significant (Bonferroni-corrected $p < 0.05$). A great majority of aspens, 79%, were alive, whereas 87% of the nest trees of all other species were dead (Table 3). Moreover, the condition of the nest tree significantly differed between the forest types ($\chi^2 = 22.0$, $p = 0.001$, $df = 6$). The difference was mainly due to lower proportions of dead trees in moist forest types compared with the other types, and it was mostly caused by the above-mentioned difference in condition between aspen and other nest tree species.

On average, 70% of cavities were excavated at a visible injury spot in the tree. This percentage significantly varied depending on the nest tree condition ($\chi^2 = 15.1$, $p = 0.001$, $df = 2$); 82% in healthy and 88% in decaying, but only 45% in dead nest trees (Bonferroni-corrected $p < 0.05$ for the pairwise differences between dead trees and other tree groups).

3.3. Size of the nest trees

The mean DBH of the nest tree was 37.2 cm (median value 36.0 cm, range 25.0–64.0 cm); and it varied from 27.8 cm in grey alder to 38.6 cm in aspen (Table 4). There was a significant difference in DBH between the tree species (Kruskal-Wallis

Table 4. Number (N), mean, standard deviation (SD), median, minimum and maximum diameter at breast height (DBH, cm) of the Grey-headed Woodpecker nest trees in various nest tree species.

Tree species	N	Mean	SD	Median	Minimum	Maximum
Aspen (*Populus tremula*)	53	38.6	9.3	36.0	25.0	64.0
Birch (*Betula* spp.)	11	35.7	1.9	36.0	33.0	39.0
Grey alder (*Alnus incana*)	4	27.8	1.3	28.0	26.0	29.0
Black alder (*Alnus glutinosa*)	2	28.5	0.7	28.5	28.0	29.0
Scots pine (*Pinus sylvestris*)	6	35.8	3.2	36.5	30.0	39.0
Total	76	37.2	8.4	36.0	25.0	64.0

Table 5. Number (N), mean, standard deviation (SD), median, minimum and maximum heights (m above the ground) of the Grey-headed Woodpecker cavity holes in various nest tree species.

Tree species	N	Mean	SD	Median	Minimum	Maximum
Aspen (*Populus tremula*)	57	8.1	3.1	8.5	1.8	16.0
Birch (*Betula* spp.)	11	7.5	1.8	6.5	6.0	11.0
Grey alder (*Alnus incana*)	4	5.0	0.6	5.0	4.5	5.5
Black alder (*Alnus glutinosa*)	2	5.8	0.4	5.8	5.5	6.0
Scots pine (*Pinus sylvestris*)	6	7.3	2.2	7.5	4.0	10.0
Total	80	7.8	2.9	7.3	1.8	16.0

test: $H = 14.5$, $p = 0.006$, $df = 4$). The DBH of grey alder was significantly smaller than the DBH of aspen (Dunn's test with Bonferroni correction: $p < 0.05$), but all other pairwise differences in DBH were insignificant.

The DBH significantly differed between the various forest types (Kruskal-Wallis test: $H = 13.3$, $p = 0.004$, $df = 3$). The pairwise differences between SWAMP and MT, and SWAMP and VT were significant (Dunn's test with Bonferroni correction: $p < 0.05$) with smaller median DBH in SWAMP, but all other pairwise differences between forest types were insignificant. The DBH also significantly differed between nest trees with various condition (Kruskal-Wallis test: $H = 6.37$, $p = 0.04$, $df = 2$); dead trees were smaller than decaying trees (Dunn's test with Bonferroni correction: $p < 0.05$), but all other pairwise differences between condition types were insignificant.

3.4. Heights of cavity holes

The mean and median heights of all cavity holes ($n = 80$) above the ground were 7.8 m and 7.3 m, respectively (range 1.8–16.0 m) (Table 5). The mean heights of cavity holes between tree species varied from 5.0 m in grey alder to 8.1 m in aspen (Table 5). The median height of cavity holes did not, however, significantly differ between the nest tree species (Kruskal-Wallis test: $H = 7.3$, $p = 0.12$, $df = 4$), but the difference was significant among the forest types ($H = 8.54$, $p = 0.036$, $df = 3$). There was also a significant positive correlation between DBH and the height of cavity holes in all nest trees (Spearman's correlation: $r_s = 0.72$, $p < 0.001$, $df = 78$).

4. Discussion

4.1. Nest tree species and their forest types

We detected one common and four less abundant nest tree species in our study, and we found that the proportions of tree species used by the Grey-headed Woodpecker depended on forest type. Overall, aspen was the most common species (70%) and a dominant in moist forests (83–92%). However, in dry forests Scots pine (67%), and in peatland forests alders (75% of nest trees) were most common nest trees. The importance of aspen as a nest tree in boreal areas is commonly emphasised (e.g. von Haartman *et al.* 1963–72, Dementiev & Gladkov 1966, Svensson *et al.* 1999, Fetisov 2017a), although there are only few quantitative studies of nest tree species within these areas.

However, Karhumäki (1979) and Karlin (1979) found that aspen dominated as nest tree species with 78% ($n = 27$) and 77% ($n = 30$) in studies in SW Finland, and Jussila (1981) with 75% ($n = 21$) in a study in central southern Finland. Moreover, in a study in southern coast of Finland, the percentage of aspen was 83% ($n = 18$; T. Pakkala, unpublished data), and 70% ($n = 20$) in another study in southern Finland just south of our study area (T. Pakkala & J. Tiainen, unpublished data). These five studies from Finland contained a total of 116 nest trees of five different species, namely aspen (77%), birch (9%), Scots pine (6%), grey alder (5%), and black alder (3% of nest trees), which were the same as recorded in our study. The percentages of nest tree species observed in these Finnish studies were also quite similar to the respective percentages in our study.

It is evident that the percentages of forest types of nest trees vary depending on the biotope distribution within each study area, which has also effects on the percentages of various nest tree species. We do not have comparable information about the biotope distributions from the areas of the above-mentioned Finnish studies. However, in the study located next to our area, the forests are generally more fertile compared with our study area especially with a larger proportion of OMT and more fertile forests (Soveri 1933). Thus, in this area, as much as 60% of nest trees located in OMT (T. Pakkala & J. Tiainen, unpublished data) whereas the respective proportion was only 17% in our study although the OMT was selected more often than expected.

In other quantitative studies from boreal and hemiboreal areas of Europe, the percentage of aspen of nest trees was 87–91% in Norway with three other, occasional tree species (Haftorn 1971, Hågvar *et al.* 1990, Stenberg 1996), and 40–95% in European parts of Russia with eight less abundant tree species (Fetisov 2017a). Local differences were also observed, e.g. in a few areas in Norway and in Russia, the Grey-headed Woodpecker was mentioned to use mainly oaks (*Quercus* spp.) as nest trees (Haftorn 1971, Hågvar *et al.* 1990, Fetisov 2017a).

In more southern, mainly temperate European areas, where various woodpecker species prefer deciduous trees for nesting, the number of nest tree species is usually larger than in boreal areas (see Hågvar *et al.* 1980, Pakkala *et al.* 2019). Glutz von Blotzheim & Bauer (1980) and Fetisov (2017a) list some 13–20 various nest tree species of the Grey-headed Woodpecker in central Europe and in Russia. In temperate areas of central Europe beeches (*Fagus* spp.) and oaks are used most often as nest trees (Conrads & Herrmann 1963, Blume 1996, Südbeck 2009), but in similar areas of eastern Europe the nest tree choice is more variable (Dementiev & Gladkov 1966, Fetisov 2017a). Aspen can also be a dominant nest tree species in some of the southern areas, e.g. in a few areas in northern Germany (Brand & Südbeck 1998), in Romania (Domokos & Cristea 2014), and in Ukraine (Fetisov 2017a).

Grey-headed Woodpeckers predominantly select deciduous tree species for nesting, but coniferous tree species, such as pines (*Pinus* spp.) (see above), spruces (*Picea* spp.), firs (*Abies* spp.), and larches (*Larix* spp.) are also used in some areas (e.g. Glutz von Blotzheim & Bauer 1980, Fetisov 2017a). In addition, nest-boxes may be used for nesting (e.g. Hortling 1929, Haftorn 1971, Glutz von Blotzheim & Bauer 1980), but these cases are apparently quite rare.

4.2. Selection of nest trees

Nest cavities in our study were mostly (85%) in decaying or dead trees. However, a great majority of aspens (79%) were living, whereas only 13% of the nest trees of all other species were alive. The proportions of living nest trees were higher in fresh forest types, where aspen dominated among nest trees. The situation was similar in the nearby study area with 93% living aspens, but only with 17% living other nest trees (T. Pakkala & J. Tiainen, unpublished data). There are no exact data of nest tree condition in other Finnish studies, but majority of aspens were mentioned to be alive in two studies (Karlin 1979, Jussila 1981). In studies with aspen as a dominant tree species the proportion of dead and dying trees was 78–87% in Norway, although 63–78% of the nest trees were still living (Hågvar *et al.* 1990, Stenberg 1996), but the respective amount living nest trees was only 38% in Romania (Domokos & Cristea 2014).

Although most aspens which were used for nest trees in our study were living, the Grey-headed Woodpeckers often (70%) selected injury spots in the tree trunk for the cavity excavation site, and these spots were especially common in still living trees (87%). In the aspens the cavity holes were often located in round, basal areas of broken branches. Similar pattern was detected in central European studies with beeches as dominant nest tree species: almost all nest trees were living, but the Grey-headed Woodpeckers regularly used injured areas, typically vertical scars in the trunk for cavity excavation (Conrads & Herrmann 1963, Blume 1996, Südbeck 2009).

The injured areas allow a suitable spot in the trunk to start the cavity excavation to the soft interior, and simultaneously the firm core with callus formation around the injured areas sustain the cavity and protect it from rain and sunshine (see Conrads & Herrmann 1963). Cavities were also located almost always in the trunk of the tree, and only occasionally in large branches, e.g. with 2.5% (this study), 0% (Kosiński & Kempa 2007), 5% (Südbeck 2009), and 13% (Domokos & Cristea 2014), which may be caused both by the location of suitable injury spots, and the selection of large trees for cavity excavation (see below).

4.3. Size of nest trees and height of cavities

We found a median DBH of 36 cm for nest trees, but grey alder was smaller than the other four tree species. Nest trees were smaller in SWAMP, and dead trees were smaller compared with decaying ones. The mean DBH of aspen nest trees in our study, 37 cm, was relatively similar to most results in studies with aspen as a dominant nest tree species: 35 cm (Hågvar *et al.* 1990; 0.5 m above ground), 36 cm (Stenberg 1996; DBH), 29 cm (Brandt & Südbeck 1998; DBH), and 35 cm (Domokos & Cristea 2014; DBH). We did not measure the diameter of the trunk at cavity opening, but in Norwegian studies it was 24–26 cm (Hågvar *et al*. 1990, Stenberg 1996), and in Russia usually 20–37 cm (Ivanchev 2005).

We observed a mean height of 7.8 m for cavity holes, although the range (1.8–16 m) and variation in the means of individual tree species (5.0–8.1 m) were relatively large, with the lowest mean values in grey alder, and the highest observed in aspen. Cavities were higher in MT than in SWAMP, which was dominated by alders as nest trees. In other studies in Finland, a mean height of 5.0 m was reported by Karhumäki (1979), 4.5 m by Karlin (1979) and 4.9 m by Jussila (1981).

In addition, the nest card data of the Finnish Museum of Natural History contained information of the cavity height of 91 Grey-headed Woodpecker's nests predominantly from southern and southwestern coasts of Finland; the mean cavity height was 5.3 m (range 1.2–12 m) in this dataset. In other European studies with aspen as the dominant nest tree, the mean cavity height was consistent with the other Finnish results; 5.6–6.4 m (Hågvar *et al.* 1990, Stenberg 1996, Brandt & Südbeck 1998, Ivanchev 2001, Domokos & Cristea 2014). In a review study from Russia, Fetisov (2017b) reported a total range of cavity height of 0.5–18 m in local studies within boreal and temperate areas in European part of Russia.

We detected a significant positive correlation between nest tree diameter and cavity height. Although the diameters of cavity trees were of the same size compared with the above-mentioned heights of other studies, cavities were higher in our study area. The large heights of cavities in our study area may be partly explained by use of higher trees, especially living aspens (T. Pakkala, unpublished data). Unfortunately, Grey-headed Woodpecker's nest tree diameters or tree heights were not recorded in previous Finnish studies. However, the cavity heights of the Grey-headed Woodpecker were comparable with those of Black Woodpecker (*Dryocopus martius*) in aspens within our study area, but the diameters of the aspen nest trees of the Black Woodpeckers were still larger (Pouttu 1995, T. Pakkala, unpublished data).

4.4. Nest tree and cavity reuse

Woodpeckers commonly use same, suitable trees for nesting in various years (see Stenberg 1996, Winkler & Christie 2002, Pakkala *et al.* 2017). We observed that Grey-headed Woodpeckers used ca. 4% of nest trees for nesting in several cavities during the study period, and many of its nest trees were also used by the Black Woodpecker and Great Spotted Woodpecker (*Dendrocopos major*) (Pakkala *et al.* 2020). However, the observed amounts of multicavity trees generally depend on the number of study years, and, especially, how often older nest trees have been systematically monitored. In comparison, percentages of multicavity trees in the Three-toed Woodpecker (*Picoides tridactylus*) and Lesser Spotted Woodpecker (*Dendrocopos minor*) were 25% and 7%, respectively, within the same study area and nearly same study period (Pakkala *et al*. 2017, 2019).

Grey-headed Woodpeckers are generally reported to use old cavities for nesting (e.g. Hortling 1929, von Haartman et al. 1963–72, Haftorn 1971, Glutz von Blotzheim & Bauer 1980), but quantitative data of cavity reuse are rare. We observed that reuse rate of old cavities was 41–44%, which is high compared with results of other European woodpecker species (see Wiebe *et al.* 2006, Pakkala *et al.* 2017, 2020), and also within the species itself: Stenberg (1996) detected a reuse rate of 4.5% of old cavities in Norway, and Südbeck (2009) that of 30% in Germany. However, Conrads & Hermann (1963) stated that most probably the Grey-headed Woodpecker excavates a new cavity only when old suitable cavities are not available, but they did not present any cavity reuse rates. Moreover, the Grey-headed Woodpecker was mentioned to excavate a new cavity more often than the Green Woodpecker (*Picus viridis*) (Glutz von Blotzheim & Bauer 1980), in which Blume (1961) detected a cavity reuse rate of 89% in Germany.

4.5. Nest trees in forest environments: the key role of large aspens

The Grey-headed Woodpecker prefers relatively large diameter, decaying or injured deciduous trees, which in managed Finnish forests are rare compared to natural boreal forests (e.g. Nilsson *et al.* 2002, Kouki *et al.* 2004, Vaillancourt *et al.* 2008). In addition, our research and other above-mentioned studies from boreal areas emphasise the importance of aspens as nest trees for the species. In our study area, the density of aspens with DBH of at least 27 cm (and thus suitable for the nest trees of the Grey-headed Woodpecker) was as high as 48 trees per ha in unmanaged forests, but only 0.6 trees per ha in managed forests (Ahola 2005). Similar differences in densities of large aspens between managed and unmanaged forest areas were also detected in studies of aspen in eastern Finland, although the densities of large aspens in unmanaged forest areas were clearly smaller compared with those of our study area (Kouki *et al.* 2004, Latva-Karjanmaa *et al.* 2007).

According to Ahola (2005), the percentage of dead aspens in aspen mappings within our study area was 36% in unmanaged forests, but only 2.6% in managed forests. Moreover, in managed forests, 38% of aspens were classified as damaged, but most of these damages were caused by browsing of the moose (*Alces alces*), which was directed predominantly to small diameter aspens (DBH < 21 cm); other types of damages were observed in 7% of all aspens. Assuming that 10% of large aspens with DBH > 27 cm are damaged in managed forests, and that a typical breeding territory size of the Grey-headed Woodpecker within the managed forests of our study area is 1–1.5 km^2 (T. Pakkala, unpublished data), we can estimate that there are on an average 6–9 highly preferable aspens for nest trees per average territory.

However, due to forest management history and habitat preferences of aspen, the observed distribution of aspen trees is patchy within the study area (Ahola 2005), and also elsewhere in managed boreal forests (e.g. de Chantal *et al.* 2005, Latva-Karjanmaa 2006). There are thus small (or occasionally bigger) clusters of large aspens, and there are relatively large forest areas without any suitable large aspen trees for the Grey-headed Woodpecker (see Ahola 2005). The high reuse rate of old cavities for nesting in our study area may indicate the scarcity of good cavity trees. The lack of suitable nest trees can thus be a limiting factor for the Grey-headed Woodpecker in managed boreal forest landscapes. Conservation and retention of groups of large aspens in main habitats, including clear-cuts, are therefore very important for the continuous availability of nest trees.

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Harmaapäätikan pesäpuiden ominaisuudet boreaalisissa metsissä

Tikkoja pidetään yleisesti metsien rakenteellisen tai lajiston monimuotoisuuden indikaattori- tai avainlajeina, koska ne kovertavat pesäkoloja, jotka ovat myöhemmin niiden itsensä ja muiden kololintujen käytettävissä. Kolopuiden ominaisuuksia on kuitenkin tutkittu melko vähän. Tämä koskee erityisesti boreaalisella havumetsäalueella pesiviä harmaapäätikkoja.

Tutkimme harmaapäätikan pesäpuiden ominaisuuksia 170 km^2:n kokoisella alueella Evolla Etelä-Suomessa vuosina 1987–2019. Aineisto käsitti 76 pesäpuuta ja niissä 80 pesäkoloa. Harmaapäätikan havaituista 118 pesinnästä 44 % oli vanhoissa harmaapäätikan koloissa. Pesiä löytyi neljäntyyppisistä metsistä, mustikkatyypiltä (MT), oravanmarja-mustikkatyypiltä (OMT, pinta-alaan nähden odotettua useammin), puolukkatyypiltä (VT, odotettua harvemmin) ja korvista. Pesäpuulajeja oli viisi ja haapa niistä yleisin (70 % puista ja

71 % koloista). Muut puulajit olivat koivu, mänty, harmaaleppä ja tervaleppä. Pesäpuiden lajisuhteet vaihtelivat metsätyyppien kesken. Haapa oli yleisin MT:llä ja OMT:llä, mänty VT:llä ja lepät korpimetsässä. 85 % pesäpuista oli kuolleita tai lahoavia, mutta valtaosa (79 %) kolopuiksi valituista haavoista oli eläviä, kun taas 87 % muiden lajien kolopuista oli kuolleita.

Suurin osa koloista (70 %) oli koverrettu näkyvästi vioittuneeseen kohtaan rungolla. Pesäpuut olivat suuria (keskiläpimitta rinnankorkeudelta 37,2 cm). Pesäkolot sijaitsivat keskimäärin 7,8 metrin korkeudella; korkeus ja rinnankorkeusläpimitta korreloivat merkitsevästi keskenään. Tulokset osoittavat suurten haapojen merkittävyyttä harmaapäätikan pesäpuina. Suurten haapojen ryhmien säästäminen ja suojelu lajin pääelinympäristöissä, niiden hakkuualat mukaan lukien, on tärkeää pesäpuiden pysyvän saatavuuden turvaamiseksi. Tämä koskee erityisesti talousmetsiä, missä sopivat pesäpuut voivat olla rajoittava tekijä harmaapäätikalle.

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